

Cladistics of the tribe Ectatommini (Hymenoptera: Formicidae): A reappraisal

ROBERTO A. KELLER

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The cladistic analysis of ectatommine ants by Lattke (1994) is reanalyzed and discussed. It is argued that Lattke's sample of taxa (in particular his choice of outgroups) is problematic because of the acceptance of unreliable previous analyses of ant subfamilial relationships. Additionally, Lattke's proposed reclassification is inconsistent cladistically. A revised matrix is presented with the addition of three outgroups and twelve characters (19 taxa and 41 characters in total). This matrix yields a single most parsimonious cladogram ($L=116$; $CI=46$; $RI=61$) with Ponerinae paraphyletic with respect to the other poneroid exemplars included (*Apomyrma*, *Cerapachys* and *Cheliomyrmex*). This result illustrates the need for a full taxonomic revision of the poneroid group.

R. A. Keller, Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853, U.S.A.

Introduction

Ectatommini Emery is a cosmopolitan tribe of ponerine ants. A series of studies by Brown (1958; 1960; 1965; 1975) culminated in the recognition of 51 genera in 11 tribes for Ponerinae. Brown (1958) redefined the Ectatommini to include 9 genera: *Acanthoponera* Mayr, *Heteroponera* Mayr, *Rhytidoponera* Mayr, *Paraponera* F.Smith, *Ectatomma* F.Smith, *Aulacopone* Arnoldi, *Gnamptogenys* Roger, *Proceratium* Roger, and *Discothyrea* Roger. This redefinition included recognition of Paraponerini (*Paraponera*) and Proceratini (*Proceratium* + *Discothyrea*) as junior synonyms of Ectatommini.

Recently, Lattke (1994) addressed the validity of Brown's revised Ectatommini applying cladistic techniques for the first time within Ponerinae. He revived Paraponerini and Proceratini from synonymy, redefined Ectatommini to include only 5 genera (*Acanthoponera*, *Heteroponera*, *Rhytidoponera*, *Ectatomma* and *Gnamptogenys*), and considered the position of *Aulacopone* as uncertain due to the lack of evidence (see below). However his analysis is inadequate in terms of his character coding and taxon sampling and his classification does not reflect the groups found on his cladogram.

The main purpose of this paper is to revise Lattke's (1994) analyses and to show that his data

provide ambiguous evidence in support of his conclusions. Secondly, it is argued that a more thorough taxon sampling will be required in order to shed some light on the taxonomic problems posed by the circumscription of Ectatommini and, in general, the tribal classification of Ponerinae.

Taxonomic history of Ponerinae

Lattke's (1994) study suffers from his choice of outgroups. In order to understand this problem a brief taxonomic history of Ponerinae is required. Ponerinae was first erected by Lepeletier de Saint-Fargeau (1835) as a family-group name. The group was simply defined as possessing '[f]emelles armées d'aiguillon. Premier segment de l'abdomen formé d'un seul noeu' (Lepeletier 1835:185). The former character is a synapomorphy for the Aculeata. The latter is a synapomorphy of Formicidae. It was later transformed into a subfamily of Formicidae by Mayr (1862) with two of spelling emendations by other authors. The contents of Ponerinae grew and changed as a result of a century of myrmecological expeditions and the acquisition of new material from previously unknown faunas. At this time, Ponerinae was not diagnosed by any derived characters and a diverse array of unrelated but plesiomorphic ants were placed there, resulting in a highly unnatural taxon.

Brown (1954) presented a summary of all taxonomic information regarding Formicidae and proposed the first explicit phylogeny of the family. Brown's diagram shows a basal divergence within the ants into two main groups that he termed the poneroid and the myrmecoid complexes. His poneroid complex included a basal group of 'primitive ponerines' with the 'advanced ponerines' budding out, together with the army ants (Dorylinae s.l.) and the myrmicines. The myrmecoid complex included all other subfamilies, and was named after the genus *Myrmecia* Fabricius that appears at the base. Later, Wilson et al. (1967) proposed the same phylogenetic arrangement with the addition of the fossil *Sphecomyrma freyi* Wilson & Brown at the base of the myrmecoid complex. Taylor (1978) presented a slightly modified diagram; he put *S. freyi* as the ancestor of all the ants and, based on the tubulation of the fourth abdominal segment, transferred the genus *Myrmecia* from the myrmecoid complex to the poneroid complex, renaming the former as the formicoid complex.

Baroni Urbani (1989) published the first cladogram for all the subfamilies of Formicidae. His analysis is unreliable because of problems in character coding and search strategy (Carpenter 1990). In addition, he treated Ponerinae as a terminal clade in the analysis even though admittedly paraphyletic due to the lack of clear autapomorphies suggesting otherwise. In summary, Ponerinae has been recognized as a paraphyletic assemblage of genera since the phylogenetic relationships between ant subfamilies were considered for the first time by Brown (1954).

Bolton (1990a; 1990b; 1990c) discovered many potential taxonomically informative characters from a detailed study of abdominal plate morphology across the poneroid group of subfamilies. Bolton's discoveries are of great importance, nevertheless the methods of interpretation he used were neither fully cladistic nor consistent. He identified sets of synapomorphies for various groups of genera and decided that those groups deserved subfamily status. Consequently, he unified *Cerapachys* F. Smith, *Acanthostichus* Mayr, *Ctenopyga* Ashmead, *Cylindromyrmex* Mayr, *Leptanilloides* Mann, *Simopone* Forel and *Sphinctomyrmex* Mayr and revived the subfamily Cerapachyinae. He transferred *Apomyrma* Brown, Gotwald & Lévièvre from Ponerinae to Leptanillinae. He also proposed the tergo-sternal fusion of the IV abdominal segment as a synapomorphy for the remaining

Ponerinae genera and dismissed as parallelism all the characters shared between some 'advanced' ponerines and members of the revived Cerapachyinae and the doryline section (all army ants). Finally, he placed Ponerinae, Leptanillinae, Cerapachyinae and the army ant subfamilies into an informal 'poneroid group', defined by the fusion of the presclerite and postclerites of the third abdominal segment. Despite Bolton's usage of cladistic terminology, these reclassifications were done without a test of congruence among data.

Baroni Urbani et al. (1992) performed a cladistic analysis using subfamilies of Formicidae as terminal taxa. This analysis was based on Bolton's recent reclassifications, but with the following further modifications: *Aenictogiton* Emery, a genus known only from males with a history of uncertain placement between Ponerinae and the army ants (s. s.) was treated as a separate terminal; *Apomyrma*, was also treated as a separate terminal, despite Bolton's recent reclassification; *Leptanilloides*, one of the genera placed by Bolton in Cerapachyinae, was also treated as a separate entry. Ponerinae is polymorphic for 41.3 % of the informative characters in the matrix. This situation reflects the heterogeneity of the ants placed inside this taxon. Figure 1 shows the resulting cladogram. This result supports the separation of the ants into Bolton's poneroid group (but see Grimaldi et al. 1997). The cladogram shows a basal polytomy inside the poneroid group involving Ponerinae along with *Apomyrma*, Leptanillinae and the rest of the poneroids. Based on that result, Baroni Urbani et al. (1992) decided to place *Aenictogiton*, *Apomyrma* and *Leptanilloides* in subfamilies of their own.

Lattke's analysis

Lattke (1994) was concerned not with the relationships among members of the poneroid group, but rather with the monophyly of the Ponerinae tribe Ectatommini. For this purpose he included all but one of the genera considered by Brown (1958) as members of Ectatommini. He explicitly excluded *Aulacopone* because of the lack of information: about 38.8% of the characters he used in the matrix. To test the monophyly of Ectatommini, he sampled representative genera from 3 out of 5 of the remaining ponerine tribes. He performed two analyses using either *Cerapachys* (Cerapachyinae) or *Myrmecia* (Myrmeciinae) as outgroups, each in a separate analysis. His matrix contained 36 morphological characters and the following taxa:

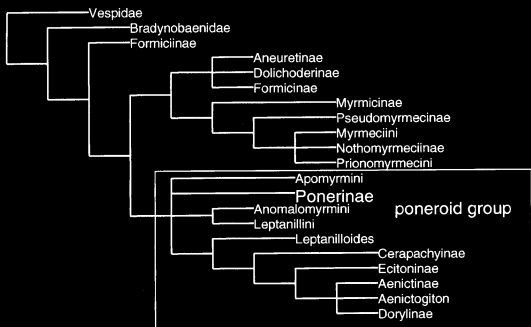


Figure 1. Consensus tree of 72 most parsimonious cladograms for Formicidae (after Baroni Urbani et al. 1992).

Ectatommini:	<i>Paraponera</i> F. Smith <i>Proceratium</i> Roger <i>Discothyrea</i> Roger <i>Rhytidoponera</i> Mayr <i>Ectatomma</i> F. Smith <i>Gnamptogenys</i> Roger <i>Acanthoponera</i> Mayr <i>Heteroponera</i> Mayr	Ponerini:	<i>Harpegnathos</i> Jerdon <i>Pachycondyla</i> F. Smith <i>Centromyrmex</i> Mayr <i>Amblyopone</i> Erichson
		Ambyoponini:	<i>Platythyrea</i> Roger
		Platythyreini:	<i>Typhlomyrmex</i> Mayr
		Typhlomyrmecini:	<i>Cerapachys</i> (1st outgroup)
		Cerapachyinae:	<i>Myrmecia</i> (2nd outgroup)
		Myrmecinae:	

Figure 2 shows the consensus cladogram of his first analysis. This is a consensus of 5 most parsimonious cladograms (C.I.=50, R.I.=62) using *Cerapachys* as outgroup. Based on this first analysis, he proposed to exclude *Paraponera*, *Proceratium* and *Discothyrea* from Ectatommini, and to revive the tribes Paraponerini and Proceratini to place those excluded genera. As for Ectatommini, he explicitly redefined it to include *Rhytidoponera*, *Ectatomma*, *Gnamptogenys*, *Acanthoponera* and *Heteroponera*. Note that on this tree (Fig. 2) the

exclusion of the 3 genera appears well founded, but that the redefined Ectatommini is part of a polytomy. This polytomy is the result of conflicting resolutions among the 5 most parsimonious trees. The redefined Ectatommini is not monophyletic under any of those resolutions. Lattke decided to leave Ectatommini, awaiting further evidence.

Figure 3 shows the result of Lattke's second analysis using *Myrmecia* as outgroup. Lattke reported only the strict consensus tree¹ for this anal-

¹Lattke reported his consensus tree as being the result of four most parsimonious trees (L=96, C.I.=48, R.I.=63). In reanalyzing his data, only two most parsimonious trees were found with the same length, C.I. and R.I. Lattke's original consensus tree is less resolved than the one presented here (Fig. 3). This fact discards the possibility of having a higher number of mpt's due to consideration of semistrictly supported trees. The two most parsimonious trees were obtained applying the mswap+ command in NONA (Goloboff 1996) that guarantees an exact solution. No explanation could be found for the difference in the number of most parsimonious trees.

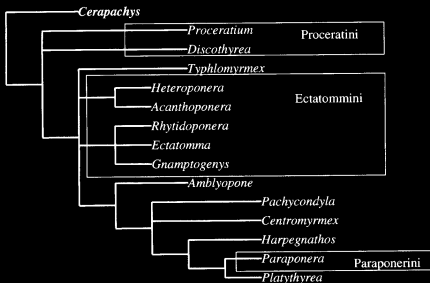


Figure 2. Consensus tree of 5 most parsimonious cladograms from Lattke (1994) with *Cerapachys* as outgroup.

ysis and made some concluding remarks about the difference in position of *Paraponera*. This result is even less consistent with his proposed reclassification. Ectatommini sensu Lattke is still paraphyletic and the tribe Proceratini is nested inside the former tribe. Moreover, if one compares the unrooted ingroup topologies from the two analyses, it can be seen that they are basically the same (they differ in resolution) but the root is placed on opposite parts

of the tree. For example, *Paraponera* is terminal in the tree using *Cerapachys* (Fig. 2) as outgroup and basal in the tree using *Myrmecia* (Fig. 3) as outgroup.

Lattke's ingroup sample is efficient in representing the variability among Ponerinae and in posing a test for the monophyly of Ectatommini. Nevertheless, his outgroup choice is problematic. Based on Baroni Urbani et al. (1992), Lattke

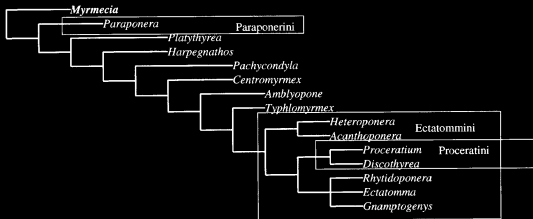


Figure 3. Consensus tree of 2 most parsimonious cladograms from Lattke (1994) with *Myrmecia* as outgroup.

choose *Cerapachys* (Cerapachyinae) as outgroup. If one takes the analysis of Baroni Urbani et al. (1992) as reliable (but see Grimaldi et al. 1997 for an opinion to the contrary), *Cerapachys* is a good choice for an outgroup; it is closely related to Ponerinae without being nested inside this subfamily and it lacks all the specializations found in the army ants. The latter situation makes homology assessment between *Cerapachys* and the ingroup more straightforward. However, as was previously discussed, the method used by Bolton (1990a) casts some doubts about the validity of his decision to revive Cerapachyinae as a group outside Ponerinae and consequently about the choice of terminals by Baroni Urbani et al. (1992).

Myrmecia is a better choice for an outgroup. It is outside the poneroid group (Grimaldi et al. 1997), and therefore does not suffer from all the problematic taxonomic history of that group. Also in comparison with other groups outside the poneroid group it still has many comparable attributes shared with poneroids. It is puzzling then, that Lattke included *Myrmecia* but ignored the result from that analysis. In any case, both outgroups should be analyzed simultaneously in an unconstrained analysis to maximize global parsimony (Farris 1982; Clark & Curran 1986; Nixon & Carpenter 1993).

Aside from the taxon sampling problem, Lattke's study contains some problems regarding the characters used. The problems range from misassignment of states to questionable decisions about character coding. The following sections present a critical reanalysis of Lattke's data, concerning both taxon sampling and character reevaluation.

Methods

Cladistic analysis was performed using the programs Nona (Goloboff 1996) and Winclada (Nixon 1999). Winclada was used to edit the data matrices and as a platform to submit the matrices to Nona. Nona was used for cladogram evaluation by applying the multiple tree search command (mult*) via random addition sequence with tree bisection-reconnection branch swapping and 50 random additions. This was followed by the 'max*' command to perform additional branch swapping. Consensus trees were calculated with Nona ('nel' command) if more than one most parsimonious tree was found. Winclada was then used to visual-

ize trees, to map changes on branches and to edit trees for output purposes. Bremer support values (Bremer 1988) were calculated for the final cladogram (analysis 3, see below) using Nona, setting 'hold' to 4,000 and applying the suboptimal command to keep trees up to six steps longer, then applying the command 'bs' to sort the pool of trees and produce the necessary consensus.

Three different analyses were performed as follows based on modification of Lattke's (1994) data.

1. The original matrix was analyzed with *Cerapachys* and *Myrmecia* included at the same time (16 taxa and 36 characters). *Myrmecia* (as Myrmeciinae) was used to orient the trees in this and all the rest of the analyses for the reasons explained in the previous section.

2. The 16 taxa matrix was revised by reevaluating each character resulting as follows: characters 6 and 24 were deleted because of ambiguous homology assessment (6, the anterior clypeal shape, is extremely variable among the taxa considered which Lattke tried to deal with by creating a five state additive character, but the additivity is not well justified and the character loses all information if treated as nonadditive; 24 describes the relative protrusion of the helcium, but this attribute is continuous across taxa and is difficult to define. Characters 9 and 15 contain states coded as 'variable'. This appears to mean polymorphic and was recoded as such. Character 35 describes the relative curvature of the gaster ventrally as: absent (0), arched on either abdominal segments III or IV (1), and arched on segment IV only (2). The distinction between states 1 and 2 of this character is vague, so these states were merged to describe only the absence (0) or presence of gaster curvature (1). All multistate characters were recoded as nonadditive because of untenable justification to the contrary. All uninformative characters were excluded from the analysis (i. e., 2, 17, 20, 21, 26, 27, 29, 31). The revised matrix contained 16 taxa and 26 informative characters.

3. Three additional taxa were included in the revised matrix. *Nothomyrmecia* Clark (Nothomyrmecinae) was chosen as an additional outgroup to include another member of the myrmecoid complex (see Fig. 1); *Apomyrma* (Apomyrminae) was included to test its placement outside Ponerinae; and, *Cheliomyrmex* Mayr (Ecitoninae) was included to represent the army ants. The inclusion of these three taxa reduced the number of uninforma-

tive characters in Lattke's matrix from eight to four. These four uninformative characters were discarded from the matrix (i. e., 2, 21, 26, 29). Information about the characters for the three additional taxa was recompiled from various bibliographic sources (Watkins 1982; Bolton 1994; Ward 1990; Hölldobler et al. 1996; Grimaldi et al. 1997). In addition, specimens of *Cheliomyrmex morosus* (F. Smith), *Myrmecia forficata* Fabricius and *M. nigrocincta* F. Smith were available for examination. The use of literature as a source of information prevented the coding of many characters for the three additional taxa. This resulted in many missing values for those taxa (43.75% of missing values for *Nothomyrmecia* and *Apomyrma*; 37.5% for *Cheliomyrmex*). These percentages include a character that is inapplicable in all three taxa. This level of missing data can weaken the application of the parsimony criterion (Nixon 1999). To minimize this problem, twelve more characters were scored based on the aforementioned studies, yielding relatively lower missing value percentages (43.18% for *Apomyrma*; 34.1% for *Nothomyrmecia*; and 27.27% for *Cheliomyrmex*). *Apomyrma* still has a high missing value percentage because four of the added characters came from males and these are unknown for *Apomyrma*. Table 1 shows the final revised and expanded matrix containing 19 taxa and 41 characters (all informative).

Results

Reevaluation and expansion of Lattke's (1994) data resulted in the following characters (all characters are from adult workers unless otherwise noted):

- Degree of fusion between the basal antennal sclerites and frontal carinae: antennal sclerites independent of frontal carinae (0); antennal sclerite fused but discernable from frontal carinae (1); antennal sclerite completely fused and not discernable. This character appears to imply a nested series of states and therefore can be treated as additive. Nevertheless, doing so only introduces ambiguity on the results, and hence was treated as nonadditive to maximize congruence. Char. 1 of Lattke (1994).
- No. of maxillary palp segments: 6 (0); 5 (1); 4 (2); 3 (3); 2 (4); 1 (5). Char. 3 of Lattke.
- No. of labial palp segments: 4 (0); 3 (1); 2 (2); 1 (3). Char. 4 of Lattke.
- Anterior clypeal lamella: absent (0); present (1). Char. 5 of Lattke.
- Funiculus: filiform (0); incrassate (1); clubbed (2). Char. 7 of Lattke.
- Promesonotal suture: flexible (0); fused and immobile (1). Char. 8 of Lattke.
- Posternal process: unilobed (0); posteriorly bifurcate (1). Char. 9 of Lattke.
- No. of stout moveable setae on the foretibial apex: 2 (0); 1 (1); none (2). Char. 10 of Lattke.
- Row of stout setae at the anterior edge of the foretarsal base: present (0); absent (1). Char. 11 of Lattke.
- Prominent seta on foretarsal base: absent (0); present (1). Char. 12 of Lattke.
- No. of mesotibial apical spurs: 2 (0); 1 (1); none (2). Char. 13 of Lattke.
- No. of metatibial apical spurs: 2 (0); 1 (1). Char. 14 of Lattke; he reported a third state, but none of the taxa included in his original matrix have this state.
- Empodia: present (0); absent (1). Char. 15 of Lattke.
- Metacoxal cavities: open (0); closed (1). Char. 16 of Lattke. See also Ward (1990b), Bolton (1990b), Baroni Urbani et al. (1992) and Grimaldi et al. (1997).
- Metabasitarsal sulcus: present (0); absent (1). Char. 17 of Lattke. See also Hölldobler et al. (1996).
- Petiol laterotergite: present (0); absent (1). Char. 18 of Lattke. See also Ward (1990).
- Petiolar tergum and sternum: not fused (0); fused (1). Char. 19 of Lattke.
- Anterior face of third abdominal segment: without a carina dorsal to the helcium (0); with such carina (1). Char. 22 of Lattke.
- Posterior border of petiolar sternite: with lateral lobes (0); lateral lobes absent (1). Char. 23 of Lattke.
- Sternum of helcium: inconspicuous (0); prominent (1). Char. 25 of Lattke.
- Abdominal III tergosternum fusion: absent (0); present (1). Char. 27 of Lattke.
- Abdominal IV tergosternum fusion: absent (0); present (1). Char. 28 of Lattke.
- Dorsal stridulatory organ: absent (0); present between segments III & IV (1). Char. 30 of Lattke.
- Ventral stridulatory organ: absent (0); present between segments III & IV (1). Char. 31 of Lattke.
- Abdominal segment IV presclerite: separated from rest of segment by a constriction (0); thickened as a distinct collar (1). Char. 32 of Lattke.
- Postpetiolar process: with a vertical anterior face and a sharp ventral edge which curves concavely posterad to join the rest of the gaster (0); with a vertical anterior face that forms an acute angle with the ventral border (1); process made up of low carina, anterior face of second abdominal segment forms a right angle with its ventral border (2); projects anteriorly as a shelf (3); absent (4). Char. 33 of Lattke.
- Jugal lobe of hind wing of queen: present (0); absent (1). Char. 34 of Lattke.
- Curvature of the gaster: absent (0); present (1). Char. 35 of Lattke, modified as described above.
- Lateral hypopygidial margins: without stout setae (0); with stout setae (1). Char. 36 of Lattke.
- Antennal sockets: inclined to almost vertical (0); horizontal (1). After Bolton (1994).
- Antennal sockets: concealed in full face view (0); exposed in full face view (1). After Bolton (1994).
- Clypeus: broad from front to back, antennal sockets far from anterior margin of head (0); reduced, antennal sockets almost reaching anterior margin of head (1). After Bolton (1994).

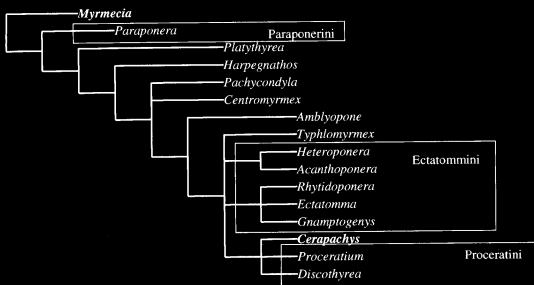


Figure 4. Consensus tree of 5 most parsimonious cladograms from Latkke's original matrix with *Cerapachys* and *Myrmecia* included. *Myrmecia* is used as outgroup.

33. Eyes: present (0); absent (1). This is char. 6 of Baroni Urbani et al. (1992).
34. Malar area in frontal view: visible (0); reduced (1). Char. 7 of Baroni Urbani et al. (1992).
35. Metatibial gland: absent (0); present (1). Char. 14 of Baroni Urbani et al. (1992).
36. Segment IV, presclerite length: < .5 IV (0); > .5 IV. Char. 24 of Grimaldi et al. (1997).
37. Spiracles of V-VIII: not visible (0); visible (1). Char. 30 of Baroni Urbani et al. (1992).
38. Male propodeal spiracle: slit-shaped (0); round to elliptical (1). Char. 53 of Baroni Urbani et al. (1992).
39. Male segment III: tergosternal fusion absent (0); present (1). Char. 54 Baroni Urbani et al. (1992).
40. Male segment IV: without presclerites (0); with differentiated presclerites (1). Char. 55 of Baroni Urbani et al. (1992).
41. Male tergite VII: sclerotized (0); desclerotized (1). Char. 56 of Baroni Urbani et al. (1992).

Results from cladistic analyses

1. Analysis of Latkke's (1994) original matrix with *Cerapachys* and *Myrmecia* (Myrmecinae) included at the same time resulted in 5 cladograms of length 103 ($L=110$ with uninformative characters added, C.I.=47, R.I.=63). The consensus is depicted in Figure 4. As expected from visual examination of Latkke's original consensus (Fig. 2 & 3), the inclusion of these two taxa results in a paraphyletic Ponerinae. *Paraponera* is the sister group of the rest of the ponerines + *Cerapachys*, and not

the sister genus of only *Platythyrea* as in Latkke's result (Fig. 2). Ectatommini (sensu Latkke) is still involved in a polytomy that does not resolve into a monophyletic assemblage in any of the cladograms. Proceratini is monophyletic only in three of the cladograms, where *Cerapachys* either appears as the sistergroup or nested inside the tribe. Additionally, Proceratini appears nested inside Ectatommini in three of the cladograms.

2. Analysis of the revised matrix resulted in 3 cladograms of length 79. The consensus is depicted in Figure 5. The changes in the matrix increased slightly the congruence among characters (from R.I.=63 in the original matrix to R.I.=66 in the revised one). The conflict among the Ectatommini and Proceratini clades disappeared, but the results are similar as in the previous analysis. *Cerapachys* appears nested inside Proceratini.

3. The final revised and expanded matrix (Table 1) yielded one cladogram of length 116, C.I. = 46, R.I. = 61 (Fig. 6). This cladogram portrays the myrmecoids (*Myrmecia* & *Nothomyrmecia*) together and a paraphyletic Ponerinae with respect to a clade involving *Apomyrma* + *Cerapachys* + *Cheliomyrmex*. Bremer values are low for most of the branches with the exception of the two clades that contain the Ectatommini genera (sensu Latkke).

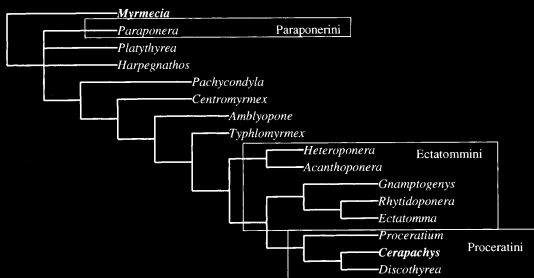


Figure 5. Consensus tree of 3 most parsimonious cladograms from recoded matrix with *Cerapachys* and *Myrmecia* included. *Myrmecia* is used as outgroup.

Discussion

Lattke's (1994) study was concerned with the ponerine tribe Ectatommini. His sample of Ponerinae genera outside Ectatommini is sufficient to challenge the monophyly of the tribe (sensu Brown 1958) and to argue for the recognition of Emery's Paraponerini. Nevertheless, Lattke's

choice of outgroup is unsatisfactory. He based his outgroup selection on a previous analysis by Baroni Urbani et al. (1992), but this analysis is problematic because it contains faults that are the result of a long turbulent history of the taxonomy of the poneroid complex as a whole.

When *Myrmecia* is chosen as outgroup (argu-

Table 1. Final recoded and expanded matrix. Missing values are denoted by '?'. Polymorphies are denoted by '*'. Inapplicable characters are denoted by '-'. All characters are treated as nonadditive.

	10	20	30	40	
<i>Myrmecia</i>	0000000000	0000001000	0000000000	0001010001	0
<i>Cerapachys</i>	0210110200	1101002011	1000121101	1100111111	0
<i>Paraponera</i>	0110000200	0000111010	1110040011	0000010001	1
<i>Proceratium</i>	0210110210	11*1111010	1100121101	0000010111	0
<i>Discothyrea</i>	2200210210	2101111011	1100121101	0000010111	0
<i>Rhytidoponera</i>	0321111100	1110111010	11*1131101	0000010111	0
<i>Ectatomma</i>	0421101100	1110111010	1110130101	0000010111	0
<i>Gnamptogenys</i>	14211*1211	1110111010	110?131101	0000010111	0
<i>Heteroponera</i>	121120*111	1111001100	1100111001	0000010111	0
<i>Acanthoponera</i>	1001200110	1111001100	1100111001	0000010111	0
<i>Pachycondyla</i>	2200100100	0001001000	11*0010001	0000010111	0
<i>Amblyopone</i>	2110100100	00*1001*10	1100021011	0000000100	1
<i>Typhlomymex</i>	1521100001	0011001010	1100121001	0010010111	0
<i>Platythyrea</i>	2000000211	0000011001	11*0120001	0000000111	1
<i>Centromyrmex</i>	2210100101	0011001000	1100020001	0010010111	0
<i>Harpegnathos</i>	2200000000	0001?11000	1110000001	0001010111	0
<i>Apomyrma</i>	0?2010?2??	??21301020	100024?001	11100-0???	?
<i>Nothomyrmecia</i>	0?2000?2??	??20?020?0	000120?000	10000-0000	0
<i>Cheliomyrmex</i>	0?2011????	??21?020?1	100004?001	1100101001	0

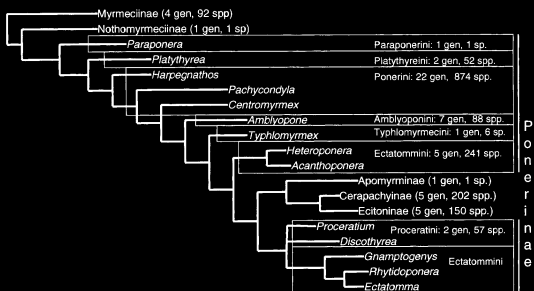


Figure 7. Cladogram from Figure 6 with the tribal grouping and numbers of currently recognized genera and species.

ably a better choice), it is clear that Lattke's preferred result is completely reversed (Fig. 3), and that his first outgroup, *Cerapachys*, is nested well inside Ponerinae (Fig. 4). Some of Lattke's characters are also problematic in the way there were coded (e. g., his character 15 with present, variable or absent). But even when the matrix is recoded the result is no different (Fig. 5). In conclusion, Lattke's results, even though they provide evidence for the reconsideration of Ectatommini, are insufficient to reclassify the group. Lattke's decision to reestablish the Ectatommini as was considered before Brown's revision of the tribe is cladistically inconsistent.

Nevertheless, Lattke's data are important because they shed some light regarding the status of Ponerinae as a natural group. When the sample outside Ponerinae is increased the paraphyly of Ponerinae is more evident (Fig. 7): the added *Nothomyrmecia* (Nothomyrmecinae) appears outside the poneroid group (a reasonable result), and *Cerapachys* (Cerapachyinae), *Cheliomyrmex* (Ecitoninae) and *Apomyrma* (Apomyrminae) group together and are nested inside Ponerinae.

Bolton (1990b) suggested the tergosternal fusion of abdominal segment four as a putative synapomorphy for Ponerinae. Nevertheless, when this

character is tested for its congruence with other characters it appears to be symplesiomorphic among the genera possessing it. The tergosternal fusion appears at the base of the poneroid group (Char. 22, Fig. 6) but it is reversed to an unfused state in the branch leading to *Apomyrma* + *Cerapachys* + *Cheliomyrmex*. This result contrasts with the intuitive view that fusion of sclerites is irreversible in evolution (Ward, 1994). Although this character loses force as a hypothesis of synapomorphy for Ponerinae, it is an additional putative synapomorphy for Bolton's poneroid group.

Figure 7 shows the final cladogram with a resumé of the tribal and family taxonomy of the groups included in this reanalysis and the number of genera and species in each tribe (Bolton 1995). The sample of characters and taxa used in this study resulted in a cladogram that does not support the tribal classification of Ponerinae as currently recognized. It can be seen that the results of this analysis are highly preliminary and that a more comprehensive taxon sampling will be necessary in order to shed some light on the poneroid group taxonomy. For example, Ponerini (Fig. 7) is only represented by 3 of the 22 genera currently recognized. Additionally, more characters of different sources are needed, as for example, characters

from larval stages, which are still very rarely used in ant taxonomy. These types of characters have already proven to be useful in other groups of Formicidae (Schultz & Meier 1995).

Latkje's study is a good step toward the understanding of Ectatommini and, in general, Ponerinae relationships. Nevertheless, much more work is still needed. Until then, the poneroid group will remain in a state of confusion.

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